ENVIRONMENTAL CAUSES OF STUNTING IN LIVING AND FOSSIL MARINE BENTHONIC INVERTEBRATES

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ABSTRACT. The various environmental causes of stunting or dwarfing in marine benthonic invertebrates are reviewed for living species and an attempt made to apply the results to cited instances among fossils. Particular attention is devoted to possible hazards of interpretation, and the criteria for distinguishing between stunted adults and juveniles among fossils is outlined. It is argued that the principal factors involved apart from food supply are the salinity, oxygen content, turbidity, agitation, and temperature of the sea water, together with population density. Palaeontological and sedimentological criteria for the distinction of these factors are proposed, but it is concluded that information on the primary factor, food supply, will continue to remain elusive to palaeoecologists.

THE stunting of growth among species of marine benthonic invertebrates by adverse environmental influences is potentially a most valuable tool in palaeoecological research, since it can provide clues to the physical environment which might otherwise be overlooked and give information on the tolerances of extinct forms. It has furthermore, an important bearing on matters of taxonomy. Unfortunately few subjects in palaeoecology are so beset with difficulties and confusion. Although there is an extensive literature, little critical analysis has been undertaken. Many authors have neglected to provide even simple measurements of fossils or criteria of maturity, thereby failing to exclude the possibility that the supposed stunted adults were actually juveniles. The sedimentary matrix has rarely been described in detail and the many different interpretations of the cause of stunting inadequately supported by reference to living animals. This should not always be held to reflect adversely on the palaeontologists concerned. Evidently in many instances stunting was of incidental interest and some worked at a time when less rigour was demanded and when the subjects of marine ecology and sedimentology were in their infancy.

Ager (1963) has preferred the term 'stunting' to the more widely used 'dwarfing' for species whose growth had been arrested or hindered by environmental influences, since the latter seems to imply a genetic control. Hence 'dwarfed organism' could best be applied to a small minority of monstrosities in an otherwise normal population, whereas environmental stunting may affect whole populations. It could be argued that the meaning of the term has in fact usually been made clear in context as signifying environmental control, but the author agrees with Ager that 'stunting' is preferable, since dwarfing suggests an extreme condition, the size being much below the normal for the species. It is certainly debatable in the present state of knowledge whether organisms of this kind are at all common in nature, but stunting in the sense of a perceptible reduction in size below the species optimum is widespread at the present day and should be a common condition among fossils. We have to bear in mind, however, that the literature on fossils is concerned primarily with forms whose size is considerably less than normal since these are the more striking.

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Certain other terms have sometimes been used. Such words as dwarf, diminutive, and micromorphic merely signify small size and should be abandoned in the context under discussion, while the term depauperate is obscure and unfamiliar, as Ager pointed out.

The observational recognition of sexual maturity should not be difficult for most living organisms but is not directly possible for fossils and one must here proceed by reasonable inference. The distinction of adults and juveniles is a necessary first step in the proper study of such faunas. If stunted fossils are to be used for the elucidation of conditions in the past, it is necessary to assume a correlation between size and environment, and that the stunting is not directly inherited (although in the long term mutants resulting in dwarfs might be favoured by natural selection). This seems more reasonable than the Lamarckian alternative on grounds of the relationship of size to food consumption, to be discussed later, and is supported by the experiments of Coe (1942) on the gastropod *Crepidula*. He found that if the objects for settlement were small the organisms remained stunted throughout life but if their offspring were transferred to experimental bottles they quickly grew to a size twenty times or more that of their parents. In the dwarfs the cells and eggs were smaller in number than average but of normal size. It is true that Ford (1928) recognized genetic control of growth in the amphipod *Gammarus* but this served merely to reduce the growth-rate and not the size at maturity.

Experiments performed by Crabb (1929) on the pond snail *Lymnaea stagnatis appressa* demonstrated clearly that while extreme crowding markedly retarded growth the individuals rapidly reached normal size after being transferred to standard conditions.

The influence of particular environmental factors on the size of marine invertebrates is not always easy to access because very few controlled experiments have been performed. One has to rely largely on inferences based on observations in a complex multivariate system, not often well documented quantitatively. It may be difficult in consequence to estimate the relative importance of different variables or isolate the significant factor. Thus Moore (1958) has pointed out that the small size of organisms in stagnant water might be due either to oxygen deficiency or to an absence of currents supplying food. Furthermore, not all variables are independent. For example, low temperature can reduce the salinity tolerance of estuarine species (Moore 1958). Because of such considerations as these, and because each species has its own environmental optimum, it is pointless as yet to seek any precise quantitative relationships from the data available. Nevertheless one can perceive a number of qualitative relationships which are likely to be of general validity, for the past as for the present.

Though this review is concerned essentially with marine organisms a few examples relating to freshwater forms are cited where the data appear to be relevant. It has also been found convenient to include ammonoids among the benthos.

FACTORS AFFECTING THE SIZE OF LIVING ORGANISMS IN THE SEA

Food supply. An obvious relationship exists between body growth and the intake of food so that it is hardly surprising that marine ecologists lay stress on the importance of this factor. If food supply is low but adequate for survival then growth will be stunted, as is apparent enough in our own species. It is desirable to make a distinction between the availability of food and the capacity of the organism to consume it. Food availability as a factor is most clearly observed among animals with an intertidal distribution. Kristensen (1957), Savage (1956), and Hancock and Simpson (1961) have all recorded a direct relationship between the growth of the suspension feeders *Cardium edule* and *Mytilus edulis* and the period of immersion, that is, the time available for feeding.

It is not clear at present, however, whether marked variation in food supply is a particularly important factor below low tide mark, since Fox's (1957) calculations suggest that generally speaking there is more than enough food available for the larger organisms in the sea, and Kristensen (1957) has estimated that current velocities of only a few centimetres per minute should be sufficient to ensure enough food for suspension feeders. On the other hand, Dr. H. B. Moore has called the author's attention to unpublished work demonstrating much slower growth of *Echinocardium* below than at low water, and he himself has found much smaller *Echinus* in deeper than in shallower water. In both cases he is inclined to believe that deficiency in food supply is the significant factor.

A gradual decrease in the size of benthonic organisms with depth of sea may possibly result from the lesser availability of food in deep water (Yonge 1961), which is probably a consequence of the progressive destruction of dead plankton on its long slow descent to the sea bottom (Emery and Rittenberg 1952), and the greater distance from river mouths. This is hardly relevant, however, to the rich populations of shallow seas, which have had the most attention and are geologically the most significant. Food supply in this case might diminish within areas of restricted circulation, where the current activity is inadequate for replenishment. Also important is the availability of suitable nutriment for organisms with specialized feeding habits. Thus Moore (1936*b*) found that the gastropod *Nucella* (= *Purpura*) *lapillus* attains a greater size at maturity on a diet of *Mytilus* than on *Balanus*.

Stunting may often result from a reduced capacity to feed because of an abnormal environment. For example, oysters and mussels may remain closed and cease feeding when conditions are adverse. *Mytilus edulis* can survive for several weeks in the absence of oxygen but does not feed (Moore 1958). The actual consumption of food is more important than its availability and is obviously the prime factor controlling size variations.

Salinity. Numerous reports in the literature suggest that abnormal salinity is one of the most potent factors inducing appreciable size reduction in marine species. Though most of this literature relates to molluscs it is apparent that a wide variety of invertebrate groups is affected, including foraminifera (Pack 1919, le Calvez 1951), ostracods (Barker 1963), amphipods (Spooner 1947), coelenterates (Rawlinson 1934, Segerstrale 1957) and echinoderms (Segerstrale 1957), so there is good reason to regard the phenomenon as general. Gunter (1947*a*, *b*) considered that salinity is by far the most important factor in producing size gradients in animals over a small area.

The most fully studied areas where the salinity differs appreciably from that of normal marine waters are estuaries such as the Tamar Estuary in south-west England (Milne 1940) and marine gulfs or inland seas where freshwater inflow from rivers and precipitation exceed evaporation. Examples include the Baltic Sea (Goldring 1922, Segerstrale 1957, Sorgenfrei 1958), the Black and Caspian Seas (Goldring 1922), the Texas coast bays (Gunter 1950, Ladd *et al.* 1957) and the Gulf of Pechili, off the Yellow Sea (Grabau 1931). All these areas are characterized by brackish water, of comparatively stable salinity in the partly isolated seas and gulfs but fluctuating considerably in salinity with tidal action in the estuaries. The marine animals that can tolerate these low salinities, dominantly species of lamellibranchs and gastropods, are frequently stunted, while stenohaline groups such as coelenterates, brachiopods, echinoderms, and cephalopods are absent or occur only sporadically. As opposed to this common restriction in size and variety, individuals are often numerous. It should be remembered that certain animals such as *Mya* and *Scrobicularia* are well adapted to brackish water and may attain their greatest size there.

The interesting experiments of Bradshaw (1957) on the foraminifer *Ammonia beccarii tepida* have yielded an apparently anomalous result, in that specimens reared in water of abnormally low or high salinity grew to slightly greater size than in normal salinity, as a result of delayed maturation.

Whilst a direct relationship between size and reduced salinity is apparent, quantitative data are sparse and difficult to interpret in the absence of more detailed descriptions of the environment. The difficulties are well illustrated by the work of Boettger (1950) on molluscs in a low-salinity inlet of the Baltic. He found no straightforward relationship between size and salinity because of the intervention of other variables such as the oxygen content of the water. These were not, however, fully evaluated. Sorgenfrei (1958) pointed out the contrast between an upper brackish and a deeper more saline zone in the Baltic waters, suggesting that the size of benthonic animals might vary to some extent with the depth of the sea floor. Moore (1936*a*) observed that the barnacle *Balanus balanoides* benefits so greatly from the increased quantity of food suspended in estuarine water and from currents bringing the food within its reach that it actually grows faster and larger in some estuaries than in the open sea. Barnacles can be used to illustrate yet further complications. *Balanus improvisus* in England was a characteristic species of brackish water, but in the Florida region it is confined to the sea, never penetrating estuaries, and *B. eburneus* takes its place in brackish waters (H. B. Moore, personal communication).

In the great majority of cases ecologists studying such low-salinity regions have been confident that the organisms they were dealing with were genuinely stunted adults. This is most obvious with sessile or semi-sessile forms but with actively vagrant animals the situation may be different. Gunter (1950) struck a cautionary note in his description of certain swimming crustaceans in the Gulf of Mexico. Many species grow up in the low salinity bays in the summer months and migrate into more open waters during the following autumn and winter. The young forms seem in fact more tolerant of low salinity than the adults. A palaeoecologist could perhaps misinterpret such regional size variations though in this particular instance the crustaceans would probably not be fossilized.

Though most of the literature refers to brackish waters there is evidence that stunting can also be induced by high salinity. Andrews (1940) observed that where evaporation raised the salinity of ponds isolated from the sea, populations of the gastropod *Neritina virginea* increased in numbers but diminished in size. Experiments by Pack (1919) on ciliates demonstrated that growth was retarded in more saline water. Many years ago Bateson (1889) made a careful study of depressions such as the Shumish Kul which were formerly connected with the Aral Sea. The depressions dried up progressively during the

Quaternary. Successive stages of evaporation were correlated with size reduction in *Cardium edule*, associated with thinning of the shell and minor changes in shape.

As opposed to this evidence, it was found during the Cambridge expedition to the Suez Canal in 1924 that only the foraminifera were stunted in the hypersaline Bitter Lakes and that several species of lamellibranchs and crabs attained the same size as in the sea (Fox 1929). It is to be observed, however, that the lamellibranch species cited are oysters and mussels, both of which have many euryhaline representatives and can presumably adapt as well to hypersaline as to brackish-water conditions. Of especial interest was the observation that a species of holothurian actually grew larger in the Bitter Lakes than in the sea, thus contradicting the general rule that echinoderms are stenohaline.

The actual cause of stunting in water of abnormal salinity appears to have received little attention. It could perhaps be a consequence of the physiological difficulties associated with osmoregulation, demanding a higher proportion of the organisms' energy and so leaving less for the intake and absorption of food. Alternatively organisms may cease feeding for long periods.

Temperature. The relationship of water temperature to the size of benthonic invertebrates is complex and frequently difficult to evaluate (Boni 1942, Tasch 1953, Moore 1958). In a review by Wimpenny (1941) it was pointed out that there is a general tendency for the size of both terrestrial and marine animals to increase with latitude, that is, with decreasing temperature, but the marine examples cited are not benthonic. Significantly, important exceptions include molluscs with calcareous shells, as exemplified by the giant gastropods and lamellibranchs of tropical seas. This may relate partly to the greater ease of precipitation of calcium carbonate in warm water. On the other hand, Coe and Fox (1944) stated that, generally speaking, lamellibranch species grow to greater sizes in higher latitudes. The same may be true of many foraminifers, and Bradshaw's (1957, 1961) experiments have thrown new light on this subject. It seems doubtful if there is any general rule for benthonic animals and each species should be considered on its merits and its optimum environmental conditions determined (Moore 1958).

The complexity is probably due largely to the interaction of opposing factors. Metabolic rates normally increase with temperature, for example in the Mytilidae, as measured by the rate of oxygen consumption (Thorson 1957), and in *Balanus*, as indicated by the rate of beat of the cirri (Moore 1958). Growth will be more rapid in warmer water, as is evident enough from the pronounced seasonal variations in the growth-rate of such well-known lamellibranchs as *Cardium edule* and *Mytilus edulis*. Coe and Fox (1944) found that the annual increment in length of certain lamellibranchs tends to be greater in lower latitudes because of the longer season available for rapid growth. As opposed to this, maturation is often later in higher latitudes so that the time available for growth during the whole life of the organism is longer (Wimpenny 1941, Coe and Fox 1944; see also Phleger 1960 and Bradshaw 1961).

Regional variations of size in relation to temperature are generally slight and often not readily recognizable (Gunter 1947*b*, Kristensen 1957). Temperature does not therefore seem to be a particularly significant factor in stunting, at least at the species level.

Oxygen content. Aquatic invertebrates differ considerably in their oxygen requirements, and experiments by Fox and Taylor (1955) on species of molluscs, worms, and crustaceans showed that some actually lived longer, and the young grew bigger, in water that was only one-fifth aerated than in fully aerated water. Pure oxygen can actually have a toxic effect. Fully aerated water is probably exceptional, however, in natural conditions on the sea bottom and it would perhaps have been more illuminating if the authors had made more realistic comparisons and discussed more fully the natural environment of the organisms under study. A pronounced deficiency of oxygen in the environment is known in fact to inhibit growth considerably, due allowance being made for certain species which are seemingly well adapted to such conditions. Stunting as a result of this factor has been recognized in foraminifera (Miller 1953, Said 1953), gastropods (Crabb 1929, Humphrey and Macey 1930), and lamellibranchs (Kindle 1930). Twenhofel (1915) described a bottom fauna in poorly aerated black muds in sheltered bays off the Estonian coast which was stunted to a fifth or a quarter of the normal size. He did not, however, evaluate the influence of low salinity.

Alternative causes of stunting in this case can be suggested. Body metabolism would be expected to diminish in conditions of low oxygen availability, and hence feeding and growth would be retarded. This is to some extent supported by the observations on *Mytilus* referred to earlier. On the other hand, oxygen deficiency is characteristic of bodies of stagnant water so that the amount of food brought in by currents would be little. This could result in the starvation of suspension feeders but could hardly be relevant to carnivors or deposit feeders since the amount of organic matter available in the bottom deposits of such stagnant bodies is normally considerable.

Turbidity. Kristensen (1957) found that both floating plant detritus, temporarily deposited on the bottom, and high silt content of the water inhibit the growth of *Cardium edule*, which apparently tends to grow faster on sandy than on muddy bottoms. Other things being equal, this differential growth will result in the attainment of larger size at maturity. Rapid growth in regions of strong currents is related to the removal of inhibiting suspended matter. The growth of *Mytilus edulis* is also, according to Kristensen, inhibited by very turbid water. According to de Lapparent (1906, p. 132) the eastern part of the Mediterranean has more stunted animals than the western; this is attributed to the influence of sediment from the Nile but it is not made clear whether or not sediment in suspension is the significant factor. Eagar (1948) quoted the results of experiments showing that silty sedimentation can kill mussels. Turbidity was in this case excluded as a factor because of the survival of forms suspended above the bottom in crates. All that appears to have been demonstrated here is the destruction of juveniles, not the inhibition of growth.

Turbidity probably inhibits the growth of suspension feeders by disturbing normal feeding activities. Thus Loosanoff and Tommers (1948) clearly showed in their experiments on oysters that when the silt content of the water was raised, the quantity of water pumped through the gills (and hence the quantity of food consumed) fell sharply. They agreed with the earlier observations of Nelson that oysters can feed in turbid water but wished to emphasize that an increase in turbidity usually causes a decrease in feeding rate. This seems to be a significant observation, since any organism which flourished on a muddy bottom must inevitably be adopted to a certain amount of turbidity.

Exposure to waves. While it has been seen that rapid water movements may aid growth of suspension feeders by removing fine sediment, extreme agitation can have an inhibiting effect.

It is relevant to mention here the results of Brown and others (1938) who studied the variation with environment of eight freshwater lamellibranch species. They found that size was greatest in almost every case in a sheltered locality and smallest in a very much exposed one, and concluded from this that wave action had a stunting effect upon growth. Gibson (1956) observed a similar relationship among scallops and suggested that excessive particle bombardment interfered with feeding. Kauffman (in press) discusses this effect of agitated water on shallow-water epifauna in general. Coe and Fox (1944) thought that storms could inhibit the feeding activity and hence the growth of mussels.

Though these various observations may have quite a general validity, it must be borne in mind that certain specialized animals are well adapted to strong wave action. *Balanus balanoides*, for example, is largest and most common in the areas of greatest wave exposure (Moore 1935). Doochim and Smith (1951), however, showed in the case of three species of *Balanus* on the Florida coast that strong currents resulted in lower growth rates and higher mortality.

Population density. It could be argued *a priori* that a high population density on the sea bottom would result in a smaller mean size of the individuals composing the population because of the relatively intense competition for food. Alternatively it could be argued that a high density of successfully settled organisms largely represented a response to an abundant food supply. Yonge (1961) made an important distinction in this respect between suspension and deposit feeders. The former can live crowded closely together if the water currents bring in abundant food whereas deposit feeders such as the Tellinaceae are more or less uniformly spaced out, each with its feeding area.

Such empirical observations as are available suggest that there may in fact be an inverse relationship between individual size and population density, both in deposit feeders such as *Tellina* (Moore 1958, p. 388) and suspension feeders such as *Balanus* (Moore 1935) and *Teredo* (Isham *et al.* 1951). Kristensen (1957) gave some quantitative data on this inverse relationship for *Cardium*. Crabb (1929) performed experiments which appeared to demonstrate this effect for certain gastropods.

Bottom sediment. Whereas the character of the bottom sediment is extremely important in controlling the distribution of benthonic communities (Jones 1950, Yonge 1961) it is in itself of limited significance in influencing growth within individual species adapted to a particular type of environment. The importance of the type of sediment lies largely in the indication it gives of the strength of the water movements and it is to this more fundamental factor that palaeoecologists should normally refer their interpretations. Among deposit feeders, however, the character of the sediment may play a more significant role, since it is the direct source of food. Thus McNulty *et al.* (1962) have found a high correlation between the size of the dominant organism and particle size among a deposit-feeding infauna in Biscayne Bay, Florida.

It is possible that a soft bottom could influence size, in that animals larger (and heavier) than a certain critical value would sink into the sediment and be suffocated, and fine mud could clog the feeding mechanisms of burrowers and hence inhibit growth, but I know of no recorded instance of stunting as a result of these factors.

Other factors. In this section brief consideration will be given to a number of factors which have been proposed at one time or another, mainly by palaeontologists, to account for stunting, but which appear to be irrelevant or of very limited application.

That depth of sea as such is unimportant as an environmental factor is demonstrated by the well-known fact that certain members of level bottom communities in shallow water in the Arctic Ocean are found at depths of 1,000 to 2,000 metres on similar bottoms in warm temperate and subtropical seas, indicating that the controlling factor is temperature (Thorson 1957).

Though Shimer (1908) suggested that the reduction in size of animals at depth might be related in part to the small amount of light penetrating to the bottom, no supporting evidence was given. The amount of light is probably important only in the special case of reef corals, since Goreau (1959) found that their growth was significantly diminished by its exclusion. He concluded that the effect of light on growth was mediated in part through the zooxanthellae.

The possible influence of hydrogen ion concentration in sea water has been referred to by several workers. Humphrey and Macey (1930), in their research on *Littorina* in tidal pools, noted a correlation between size and pH, though it is not clear how rigorously they excluded other factors such as oxygen content and salinity. Lalicker (1948) also stated that the size of the ciliate *Paramecium* decreased with pH, but remarked that the low pH values were often associated with abundant decomposing organic matter. This introduces the possibility that oxygen deficiency rather than pH might have been the significant factor involved in the size reduction. Scott (1948) suggested that low pH was a prime factor in stunting, quoting the work of Humphrey and Macey. He also referred to some experimental observations indicating that acid-toxic waters lower the absorptive capacity of the gut epithelium in certain lamellibranchs, so that stunting would be a natural consequence. Be this as it may, such observations have little relevance to sea water, which has a very constant, mildly alkaline pH owing to the buffering action of the calcium carbonate–bicarbonate–carbon dioxide system.

The chemical composition of sea water is normally very constant and is unlikely to have differed appreciably in the comparatively recent geological past, since the time that highly organized invertebrates first appeared. Hence various suggestions by palaeontologists that abnormal concentrations of certain ions might have caused stunting in fossils have an air of implausibility. Much has been made, for instance, of the observations of Sarasin (1913, 1917) in support of the idea that a high concentration of iron can have an adverse effect upon growth. Sarasin discovered that certain ponds with a rock substratum rich in iron contained minute gastropods, crabs, and fish that were supposedly stunted. No chemical analyses of the water were given, however, nor the possible influence of other factors considered. There remains, moreover, the considerable doubt whether the restricted and perhaps rather special environment of these ponds has much relevance to conditions in the sea.

Similar doubts surround the experiment cited by Loomis (1903) in which small tadpoles, fish, and snails were kept in an aquarium in which the water was saturated with an iron compound; all the individuals showed stunting effects after several months. One would like to have known more about the degree of oxygenation and the availability of food compared with the natural environment before accepting that the iron was the principal cause of stunting. Again, such experiments as this are irrelevant to conditions in the sea, where the water is never saturated with iron compounds. Moreover, the significance of iron concentration is doubtful, since it is its availability in chelated form and not its total quantity that matters (H. B. Moore, personal communication).

It may be true that the presence or abundance of certain cations such as 'Cu' retard or stop growth (Tasch 1953), though this is denied for crustaceans by Scott (1948), but again the claim is open to the charge of irrelevance. Tasch proposed, furthermore, that the water polymer trihydrol, produced by melting ice, might have an important influence, based on experiments on the growth of diatoms. No evidence was adduced that this is true also for benthonic invertebrates and no marine ecologist has, to my knowledge, ever suggested this. Similar doubts surround Tasch's suggestion of the possible importance of sulphoxide and sulphhydrol.

Grabau (1931) thought that the high magnesium chloride and sulphate concentrations in the Gulf of Pechili might have played a role in the stunting of a number of invertebrates but such stunting could in this case be merely the consequence of reduced salinity (see above).

Another suggestion favoured by a number of palaeontologists relates to the existence of 'algal meadows' in very shallow waters. Dr. Fergusson Wood has kindly offered the following statement. 'So-called "algal meadows" consist of either true algal meadows or meadows of sea-grasses. The former grow attached to a rock substrate or on a sediment in the littoral or supra-littoral. In the first case they consist of brown algae such as *Fucus*, *Hormosira* (in the Southern Hemisphere), *Sargassum*, or as algal "forests" of *Ecklenia*, *Laminaria* or *Macrocystis*, or of coralline red algae, particularly in warmer waters. The latter are usually filamentous green algae such as *Enteromorpha*, *Chaetomorpha*, *Halimeda* &c. or blue-greens such as *Oscillatoria* or *Lyngbya*. This community frequently has a reducing layer below and the algae are possibly capable of photoreduction of CO_2, getting the hydrogen from H_2S rather than H_2O. The sea-grass meadows usually have an oxidized layer at the surface of the sediment and a reduced layer or region below. The most important association, however, is frequently the epiphytic community which consists of diatoms, blue-greens, and red algae such as *Ceramium*, *Polysiphonia* and *Lawrencia* which may outweigh the sea grass.'

'Algal meadows' provide a multitude of micro-environments harbouring a rich and highly diverse animal life dominated by the epifauna. The fauna may be small as individuals, as apparently in Messina Harbour (Fuchs 1871). Fuchs maintained that this was the consequence of the concentration of juveniles in the meadows as a result of the physical exclusion by the algae of larger forms. If this interpretation is correct it obviously has nothing to do with true stunting. Evidence of stunting of mature individuals in any algal meadow appears indeed to be lacking at present.

INTERPRETATION OF STUNTING IN FOSSILS

Criteria for establishing maturity. The palaeontologist is naturally handicapped in the recognition of stunting because he cannot prove conclusively that given fossils represent sexually mature organisms. The most he can hope to do is make a reasonable case by establishing (*a*) that the suspected stunted fossils differ only in their smaller size from other forms of the same geological age, suggesting that they may belong to the same species, and (*b*) that the characters of the fossil shells correspond with those of sexually mature living organisms. Unless this is done the sceptically minded can maintain either that the small fossils belong to naturally small species or that they represent juveniles.

Fortunately in many invertebrates there are a number of criteria for establishing maturity with a considerable degree of confidence. Seasonally produced growth rings can be used in two ways. At the onset of maturity the growth of invertebrates generally tends to slow down rather than cease and this can lead to the crowding of growth rings. Vogel (1959*b*) has made use of this fact to demonstrate by graphical means stunting in living lamellibranchs and brachiopods.

Secondly, the spacing of growth rings can give useful information. In the course of a study of a Jurassic ironstone I came across a thin band of rock containing abnormally small specimens of two common lamellibranch species. A graphical study of the spacing of the growth rings showed that those of the small individuals were appreciably closer together than in larger forms elsewhere in the ironstone, suggesting that they were in fact truly stunted (Hallam 1963).

The suture lines or the septa of ammonoids can be treated in a similar way. It has often been remarked that adults exhibit a crowding together of the last few suture lines. It is probably more reliable in this case, however, for reasons to be discussed later, to use the technique proposed by Vogel (1959*a*), who plotted the amount of septal separation against whorl diameter for some Cretaceous ammonites and was able by this means to demonstrate a probable case of stunting.

While growth-ring studies are most applicable to lamellibranchs and brachiopods they may prove useful in some other groups as well. Annual growth rings have, for instance, been recognized in corals and in the genital plates of echinoids.

Adults may possess distinctive morphological features, such as the thickening of the apertural margin in some gastropods. Callomon (1957) gave several morphological criteria for the recognition of mature ammonites. Provided comparison can be made between suspected stunted and normal forms apparently of the same species in different facies of the same age, the number and arrangement of, for instance, septa in corals, chambers in foraminifers and whorls in gastropods may be significant, though this is a field requiring much further study.

In the description of suspected stunted fossils it is important at least to give both the range and mean of some measure of size. Tasch (1953, 1957) would go further and advocated plotting graphically the complete size-frequency distribution for given species. While this seems desirable where material is abundant and easily collected, the interpretation of such distributions can be more complicated than Tasch evidently appreciated in his study of a Pennsylvanian shale. For example, in the case of the lamellibranch *Nuculana bellistriata*, Tasch found that the size distribution fell into two distinct groups. The main group was unimodal but there were a few much larger specimens. These two groups were interpreted as juveniles and adults. It could equally well be, however, that a small percentage of the total could have experienced pathological gigantism (cf. Boettger 1952) and a large proportion could have been adults.

Again, the brachiopod *Crurithyris planoconvexa* showed a unimodal distribution. Tasch contrasted this with the multimodal distribution of a living brachiopod species described by Percival (1944) and suggested that therefore there were only one or possibly two juvenile stages represented in the *Crurithyris* sample. It is inadmissable, however, to compare fossils accumulated through a large quantity of sediment in perhaps a considerable time with a living brachiopod sample, only a few years old, collected from a few square metres of ground. Size-frequency distributions are, moreover, the result of the interaction of a number of variables which are not always easy to disentangle (Craig and Hallam 1963).

It must be admitted that if the various claims of stunting in fossils are subjected to the sort of tests outlined above, few could be considered proven conclusively. Indeed, Tasch (1953) went so far as to dismiss virtually all the cases he reviewed on grounds of insufficient evidence. While one can only endorse the request for fuller documentation, it is felt that Tasch has been unduly sceptical.

In the remainder of this article an attempt will be made to evaluate some of the claims of stunting in the light of our present knowledge of marine ecology and sedimentology, and make judgements on their relative plausibility. It would be tedious and rather pointless to consider each example in detail since so many authors have omitted critical data, even when one suspects that they could have made a convincing case. Interpretation at present is necessarily tentative and a whole series of detailed reinvestigations is called for. It should be stressed, however, that a too-ready dismissal of stunting for fossils of abnormally small size for the species may create more problems than it solves.

Abnormal salinity. It should not be difficult to recognize stunting in fossils that is the result of low salinity because brackish-water faunas have a distinctive character. They are normally restricted in variety, stenohaline groups being rare or absent. The euryhaline forms that dominate are largely composed of a few species of lamellibranchs, gastropods, and ostracods which may be numerous as individuals. Stunting of the molluscs together with other forms should occur, though it must be borne in mind that certain species may have been well-adapted to brackish water and attained their greatest size there. The sediments containing the fossils may give some indication of the proximity of rivers, such as deltaic sands with drifted plant remains (Schmidt 1951).

In the case of late Mesozoic and younger rocks it may be possible to utilize genera or even species, the salinity tolerance of whose modern relatives is well known. Goldring (1922) compared the Pleistocene fauna of the Champlain and St. Lawrence Valleys with that of the Baltic Sea and argued convincingly that the changing character of the former was the result of a southward decrease in salinity in the seas of that time. Gekker (1957) has reported salinity control of the fauna of the Palaeogene Ferghana Gulf in central Asia, brackish-water conditions being marked by the absence of nummulites, brachiopods, and cephalopods, and the rarity and small size of echinoids and corals. The lamellibranchs and gastropods were large in number but few in species and exhibited stunting. A group of Cretaceous molluscs in Maryland gave indications of low salinity conditions by an association of stunted marine forms with accepted brackish-water forms (Vokes 1948).

Barker (1963) has recently made a study of size variations among ostracods of the genus *Fabanella* in the Portland and Purbeck Beds of Buckinghamshire. He was able to discount the factor of mechanical sorting and related a decrease of maximum size up the succession to a reduction in salinity, by taking into account the character of the associated fauna.

Dunbar (1941) quoted a relevant example from the Permian of the Soviet Union. As the Kazanian strata are traced eastwards across the Russian Platform richly fossiliferous marine limestones pass into continental red beds via a transition zone characterized by reduced variety and apparent stunting of the fauna. Although this is attributed to brackish-water conditions one wonders whether it might rather be a case of increased salinity, bearing in mind the rich evaporate deposits near the Urals.

There is some doubt concerning Grabau's (1931) attribution of the Permian Jisu Honguer Limestone of Mongolia to deposition in brackish water. Although widespread stunting was claimed on the basis of comparison with similar species of the same age elsewhere, the fauna is composed largely of brachiopods together with a few corals and bryozoans, groups which at the present day are notably stenohaline.

Hypersaline faunas should have characteristics similar to those of brackish water but should be distinguishable by the occurrence of evaporites in the associated sediments. A possible example of such a fauna was described from the Muschelkalk of Selva Nera by Hohenstein (1913). It is composed mainly of lamellibranchs and gastropods together with a few brachiopods and cephalopods; corals, bryozoans, and echinoderms are absent. Hohenstein interpreted the small size of the fossils (1 to 45 mm.) as the result of stunting in conditions of high salinity, as suggested by the presence of gypsum and anhydrite.

Trechmann (1913) described a likely case from the Permian Magnesian Limestone of Durham. In the so-called Shell–Limestone Reef an impoverishment of the fauna is discernible up the succession. Brachiopods die out, leaving a fauna considerable in numbers but restricted in variety, composed of lamellibranchs and gastropods; some of these are apparently dwarfed. Thus species of *Pleurophorus* are only about one-third of their normal size. Taking into consideration the lithological evidence, Trechmann related this dwarfing to an increasing amount of sulphates in the sedimentation.

Arkhangel'skaya and Grigor'yev (1961) briefly allude to fossil stunting in deposits of the Lower Cambrian evaporites of Siberia.

Temperature. From what has been said earlier it seems unlikely that temperature changes can have effected appreciable variations in the size of fossil species, at least in adjacent rock formations. They should nevertheless have had a discernible effect if large enough regions are considered. An example (not strictly at the level of species) is the well-known case of the Cretaceous rudist lamellibranchs, which grew to considerable size in the Mediterranean province, in the region of the old Tethyan seaway. Associated with large, thick-shelled gastropods and large foraminifera, their growth can reasonably be related to high water-temperatures, but northwards in Europe (into presumably higher latitudes) their size diminishes appreciably (Dacque 1915, pp. 423–4).

It may prove possible to detect regional changes in size which are the result of temperature differences by correlating them with gradients of diversity (Fischer 1961, Stehli and Halsey 1963) since it is well known that organisms become progressively richer in variety towards the equator. Fischer notes that this is more marked in the epifauna than in the infauna. No confusion should arise between gradients of this sort and those that are the result of abnormal salinity. Unlike the latter, temperature gradients will probably only be detectable by the consideration of whole continents, and stenohaline animals will persist even in the regions of least diversity. However, it should be borne in mind that significant changes in size might only be recognizable at the level of genera.

Size gradients with temperature among more than a few elements in the fauna are unlikely to be common, as the optimum conditions for different species are likely to have varied considerably. This situation contrasts markedly with that concerning, for instance, abnormal salinity, since the optimum here will correspond with normal marine conditions for the bulk of the fauna.

Finally, if suitable shell material is forthcoming, it may be possible to determine their temperature of formation from the oxygen isotope ratios, and thence compare size and temperature directly.

Oxygen deficiency. Stunting as a result of oxygen deficiency is to be expected in seas where the water circulation is severely restricted and hydrogen sulphide generated by sulphate-reducing bacteria. The bottom sediments associated with this type of environment are characteristically fine-grained because of deposition in quiet water and rich in unoxidized organic matter and iron sulphide, produced by the reaction of hydrogen sulphide with iron salts in solution. An association of bituminous and/or pyritic shales with small-sized, apparently stunted fossils has indeed been repeatedly recognized (Grabau 1917, Price 1920, Scott 1924, Marr 1925, Chao 1927, Ruedemann 1935, Williams 1937). Broadhurst (1959), in a careful study of some non-marine lamellibranchs from the Upper Carboniferous of Lancashire, found an inverse correlation between shell size and the quantity of pyrite in the sediment. He interpreted this as stunting in conditions of oxygen deficiency and perhaps reduced food supply.

Though this association is impressive and probably significant, documentation is unfortunately slight and criteria of stunting rarely adduced. Fisher (1951) is a welcome exception in that he studied the beak features of brachiopods and the growth lines of lamellibranchs to deduce stunting in a rich fauna collected from iron sulphide concretions. While, moreover, most authors have attributed the stunting to oxygen deficiency, Grabau (1917) related it without good evidence to estuarine conditions for the dark Genesee Shale, and Scott's (1940) interpretation seems somewhat confused. Discussing small pyritic ammonites from the Cretaceous of Texas, which he had earlier (1924) interpreted as stunted forms, he remarked (p. 311) that many specimens were probably preserved inner whorls of large specimens, but on the next page he stated that 'many of them are obviously dwarfed'.

In cases where the preservation of pyritic micromorphs precludes the sure recognition of maturity it should not necessarily be assumed that they represent juveniles. On the other hand, a danger of misinterpretation arises from the possibility that small shells may have been preferentially pyritized. If larger shells have not been well preserved the pyritic specimens alone may have found their way into museum collections and give a misleading impression of the composition of the original fauna. Associated moulds, impressions or calcitic fossils should therefore always be sought. Kummel (1948), for instance, discussing ammonites from Texas, observed that pyritic micromorphs occur in the same beds as larger forms preserved in calcite, and Callomon (1957) pointed out that the so-called micromorphic ammonites in the Oxford Clay of Buckinghamshire are actually the pyritized nuclei of immature shells with non-pyritized body chambers.

Kummel (1948) also expressed scepticism about a claim by Jaworski (1923) of stunting in small cephalopods collected from Triassic bituminous cherty limestones in Peru. According to Kummel they appear to be of the normal size for the species and genera.

Besides more data on the fossils a proper appreciation of the evidence of the rocks is required. That not all black shales were laid down in a poorly-aerated environment is indicated, for example, by the rich benthonic fauna, including burrowers, of the

Devonian Hunsrückschiefer (Richter 1931). Pyrite usually forms diagenetically within fine-grained sediments and is not necessarily relevant to conditions in the bottom waters, though it is probably true in most cases that an abundance of pyrite signifies a poorly aerated sediment surface. The surest indication of anaerobic or near-anaerobic conditions is a fine lamination produced by alternations of organic matter with clay and calcite, probably annual in origin, as found for instance in the deeper parts of the Black Sea (Archanguelsky 1927). Laminated shales or limestones of this type are frequently barren of benthonic fossils except for extremely thin layers of nektonic animals or surface-livers, which can sometimes be shown to be stunted (Hallam 1960); alternating phases of anaerobic and poorly aerated water are implied.

One of the most detailed studies of a small-sized fauna in a formerly pyritic shale was undertaken by Tasch (1953, 1957). The Pennsylvanian Dry Shale of Kansas now contains limonite rather than pyrite because of subsequent oxidation and Tasch considered that the original environment was in fact poorly aerated. He nevertheless discounted the possibility of stunting in all but a few instances on the basis of his analysis. Since his work has important implications it needs scrutinizing in some detail.

Tasch collected some 4,000 fossils, mostly goniatites, brachiopods, and lamellibranchs. Almost the whole fauna was of pebble grade, mostly ranging between 4 and 8 mm. For the goniatites Tasch used the crowding of the last few suture lines as an index of maturity. Among 205 usable specimens of *Imitoceras grahamense* 30 were considered mature but, peculiarly enough, the size range of these approximated to that of the supposed juveniles. This paradox could be resolved by accepting that the bulk of the sample consisted in fact of mature specimens. From the data given it is far from easy to assess maturity on the basis of suture-line crowding since this is highly variable and can be repeated during the growth of a single individual, as the author has found also in certain Jurassic ammonites. Similar considerations apply to the other goniatite studied in detail, *Goniloboceras goniolobum*, interpreted as consisting entirely of juveniles though not many suture lines were visible. It would be better to make sagittal sections and use the ingenious technique of Vogel (1959*a*) of plotting septal spacings against size for normal and suspected stunted ammonoids. Doubts concerning the use of size-frequency distributions in the brachiopods and lamellibranchs have already been alluded to. One can nevertheless follow Tasch's interpretation and see where it led him.

Tasch was faced with the problem of accounting for an assemblage consisting largely of juveniles. This he did by invoking mass catastrophe, resulting in high juvenile mortality, and selective size-sorting by currents. The stunted *Imitoceras* required a further explanation based on the supposed toxic action of ionic iron in the sea water. All these explanations are open to objection.

The sort of catastrophic destructions of benthonic animals known to marine ecologists are normally intermittent, short-lived events. If such events leave any clear record at all in sedimentary successions, it is more likely to be as thin bands of fossils of all sizes, both juveniles and adults (cf. Hallam 1961) than as juveniles scattered through a whole rock unit such as the Dry Shale. The latter would imply a series of catastrophes continued over a long period of time, with recurrent repopulation from another region. It is dubiously justifiable, furthermore, to invoke size-sorting by currents without independent evidence. The work of Craig and Hallam (1963) on modern shells suggests that this process cannot be assumed without evidence even for high energy environments and is much less likely to have been important in the low energy environment signified by the formation of shale. One would also expect the larger shells to remain behind and the smaller to be carried away, yet Tasch, in his analysis of *Crurithyris*, made a direct comparison with Percival's (1944) work on living brachiopods fixed by pedicles in attempting to prove the juvenile composition of the fauna.

Finally, from what has been said in an earlier section, it is improbable that ionic iron can attain toxic concentrations in sea water. Why, moreover, should only a small fraction of the fauna be affected?

While the presence of some juvenile stages is not denied, it is surely more reasonable to explore further the possibility that the Dry Shale fauna was stunted as a result of oxygen deficiency, since Tasch himself did not deny the existence of a poorly aerated environment. This interpretation has at least the advantage of being economical.

Turbidity. Many palaeontologists are familiar with the fact that fossil species are frequently larger in rocks deposited in a relatively high energy environment, such as sandstones and calcarenites, than in shales. Examples can be cited from the Lias in Britain. The Frodingham Ironstone, a limonite oolite, contains lamellibranch species that are appreciably larger than in shales of the same age (Hallam 1963). The same is true for the Hettangian Sutton Stone in Glamorgan, which is a calcarenite deposited close to an old shoreline, above surf base (Hallam 1960). A possible example among the foraminifera is given by Lalicker (1948). *Heterostegina texana*, of the Oligocene of Texas, attains a greater size in calcareous sandstone than in shale, but in this case the factor of current sorting has to be considered.

These facts suggest the possibility of a control on growth by the turbidity of the bottom water, in cases where oxygen deficiency can be ruled out by the presence in the shales of a rich benthonic fauna including burrowers and by the absence of lamination or bituminous matter.

Species may also be larger in slowly deposited fine-grained rocks such as certain calcilutites as compared with thicker, more argillaceous successions. A high rate of sedimentation has been invoked as a cause of stunting both by Bradley (1921) and Eagar (1951) but this is probably only important in that it may signify increased turbidity.

It should be remembered that the turbidity effect has only been demonstrated as yet for suspension feeders.

Strong wave agitation. The author knows of only one case where stunting in fossils was related to extreme water disturbance. Croneis and Grubbs (1939) described the fauna collected from ellipsoidal calcite nodules in a fine-grained Silurian dolomite in Illinois. They provided what appears to be good evidence for stunting. Thus brachiopods of one-third normal size have mature pedicle structures; crinoids with calices not greater than 2 mm. have a complete cyclic arrangement of basals and radials with well-developed arm sockets, just like the mature forms of larger specimens elsewhere; gastropods, ranging in size up to 12 mm., have the same number of whorls as their more characteristic but larger relatives.

Their interpretation, however, that the nodules were formed directly by storm action, is highly questionable. From the illustration and description given, the nodules appear to be diagenetic rather than syngenetic in origin. The evidence cited for the latter, the bending of shaly laminae around the nodules, can easily be accounted for by differential compaction. Though storms may periodically stir up sediment in environments of shallow-water carbonate mud deposits such as the area west of Andros Island on the Bahama Bank (Black 1933), there is no evidence to suggest that they result in the formation of balls of calcareous mud. It is furthermore extremely unlikely that such balls would preserve their identity for long.

A more likely case of stunting in agitated water is given by Kauffman (in press) in his description of some Cretaceous oysters.

Exposure to waves may conceivably have some bearing on possible cases of stunting in reef limestones, such as described for a rich Middle Triassic fauna by Jekelius (1935). The author has also seen a peculiar micromorphic brachiopod assemblage in the Upper Jurassic sponge reefs of southern Germany, and the so-called Upper Coral Bed of the Middle Jurassic of the Cotswolds contains a rich fauna of minute brachiopods which may be stunted (Richardson 1907).

In contrast to the normal faunas of most rocks deposited in high energy environments, certain oolites have been found to contain abnormally small-sized assemblages and it is perhaps relevant to discuss these here.

The classic example is that of the fauna of the Mississippian Salem Limestone of Indiana described by Cumings *et al.* (1906). Stunting of this rich fauna, which includes blastoids, brachiopods, bryozoans, corals, gastropods, lamellibranchs, and trilobites, was claimed on the basis of the minute size of the fossils compared with similar forms in the adjacent rocks. The Salem Limestone has traditionally been considered an oolite but Patton (1953) has pointed out that true ooliths are rarely found and it should rather be described as a bioclastic limestone exhibiting a high degree of size sorting. Patton considered that the fossil content has been determined largely by particle size rather than by the character of the organic life. This interpretation seems to be borne out by the fact that both the foraminifera (of the genera *Endothyra* and *Plectogyra*) (Lalicker 1948) and the ostracods (Scott 1948) are of the normal size for their species. That wave and/or current sorting rather than dwarfing is responsible for the small size of the fossils seems plausible enough for this type of rock, but Cloud (1948) has remarked that some at least of the minute brachiopods have adult beak characters. More work on this interesting fauna is clearly desirable.

Loeblich and Tappin (1964) have recently queried the interpretation of the Salem endothyrids as normal forms because of their large size, citing the work of Bradshaw (1957) to suggest that abnormally large foraminifers may signify unfavourable conditions. Though this is conceivable, it should be borne in mind that Bradshaw's experiments, illuminating as they were, dealt only with one species, and the size differences perceived in a wide range of salinities did not exceed 5 per cent. of the maximum.

In the case of another Mississippian oolite, foraminifera of the genus *Plectogyra* do appear to be genuinely stunted (Lalicker 1948), while Stauffer (1937) has described a fauna of small gastropods and cephalopods in a silicified dolomite oolite in the Ordovician of Minnesota but no evidence supporting stunting was put forward.

A further example of an oolite containing a minute-sized fauna (lamellibranchs and gastropods) was cited from the Middle Jurassic of the Cotswolds by Arkell (1933, p. 272). This fauna was interpreted, however, as consisting of juveniles concentrated by the sorting action of currents.

High population density. Stunting as a result of high population density would be very difficult to substantiate for fossil assemblages, though it has been proposed for different faunas by Cumings *et al.* (1906), Kühn (1936), and H. and G. Termier (1951). This is principally because fossils are only rarely preserved in their positions of life, having in most cases been repeatedly disturbed by water movements and the activity of burrowers prior to ultimate burial. Local variations of shell density in fossiliferous rocks are normally held to reflect differences in rate of sedimentation and hence have little bearing on the original space conditions of the living organisms.

Abnormal ionic concentrations. Although appreciable changes in the chemical composition of sea water can effectively be discounted, the accumulation of iron and phosphate ions in toxic quantities has been proposed on several occasions to account for particular examples of fossil stunting.

Loomis (1903) made a classic study of stunting in the fauna of the so-called pyrite layer of the Tully Limestone in the Devonian of New York State. Among over fifty species of varied animals stated as including adults, few exceeded 2·0 mm. in size. Stunting was in part attributed to a high concentration of iron in the sea water, as evidenced by the abundance of pyrite. However, the amount of iron in pyrite in modern sediments bears little relationship to the amount dissolved in the adjacent sea water, in fact may vastly exceed it, coming perhaps mostly from the solution of diatoms within the sediment (Emery and Rittenberg 1952). Accepting the stunting as genuine (and no one has yet disproved it) another explanation must be sought.

That high sulphide concentration and hence oxygen deficiency is in fact responsible is suggested both by the facts cited earlier and by the special case of the Snap Band in the Frodingham Ironstone. This pyrite-rich layer contains small lamellibranchs that appear to be stunted compared with the large shells in the normal ironstone, in which limonite (an alteration product of chamosite) is the dominant mineral (Hallam 1963). Similar probable misinterpretations were made by Marr (1925) and Tasch, whose work has already been discussed, while Ager (1956) related brachiopod stunting in the Marlstone Rock-bed ironstone to an enrichment of iron in the sea water.

An association of apparently stunted faunas with phosphatic deposits has led Ladd (1925), Branson (1930), and Ball (1935) to relate the stunting to high phosphate concentrations in the sea water, but the existence of phosphate-rich deposits by no means implies greatly enriched phosphate in the bottom waters (Bushinski 1964). Almost all dissolved phosphorus brought by rivers into the sea is immediately assimilated by the plankton and subsequently deposited on the bottom after death of the organisms. Solutions within muds deposited in the Bering Sea contain thirty to ninety times more phosphorus than the bottom waters and Bushinski attributed the formation of phosphorite layers to processes of diagenesis. In the case of the Maquoketa Shale of Iowa described by Ladd (1925), in which the rich fauna has an upper size limit of 6 mm., an abundance of pyrite was also noted. Here, as in the case of the Tully Limestone, one can see that an alternative explanation of the stunting is available.

'*Algal meadows.*' It has been observed earlier that while algal (or sea grass) meadows may perhaps account for a concentration of juvenile organisms in certain cases there is no evidence as yet that they are responsible for extensive stunting. Nevertheless, Kutassy (1930) proposed this as an explanation of stunting in a fauna from lignite-bearing sediments in the Miocene of Hungary. Stunting was recognized by comparison with normal Miocene species elsewhere, but as the fauna is characterized by numerous lamellibranchs and gastropods of normal marine types together with a very small number of species of echinoderms, bryozoans, and corals, the alternative of low salinity conditions should have been fully explored, especially as this is just the sort of environment suggested by lignitic beds.

Fuchs (1871) thought that the diminutive character of the rich Alpine Triassic fauna of St. Cassian could be the result of selective exclusion of adults as in Messina Harbour, but Boni's review (1942) suggests that some species at least are genuinely stunted, though the evidence presented is not entirely satisfactory.

Kühn (1936) attributed the small size of a Middle Miocene fauna to stunting because of competition for food and living space in algal meadows, but the paucity of data makes it impossible to assess whether or not adult forms were present. The richness in epifauna (corals and bryozoans) does perhaps in this case support the possibility of algal meadows.

A provocative hypothesis was put forward by H. and G. Termier (1951) to account for the smaller size in shales than in limestones of many goniatites. As they thought that the shell characters of the goniatites in carbonaceous shales signified immaturity they proposed an environment of algal meadows which could have served as developing grounds for the young (cf. Bauer 1929). This is conceivable because goniatites were probably fairly active swimmers, but the Termiers felt obliged to interpret the small lamellibranchs and gastropods in the same beds as adults stunted because of isolation and crowding. Unfortunately little evidence was provided for distinguishing adults from juveniles and an application of the techniques proposed by Vogel (1959*a*, 1959*b*) could here prove very rewarding.

No writer on the subject of algal meadows has paid much attention to the problem of inferring their existence from the sedimentary record, which is clearly desirable if a convincing case is to be presented. Bauer (1929), describing *Posidonia* meadows in the Mediterranean, stated that they only occur where large stones are available in sand as attachment surfaces. Over the course of time black sulphurous mud rich in organic matter accumulates in the sheltered environment created by the seaweeds. A sediment of mixed stones, sand, and mud should therefore result and the associated facies should indicate the proximity of a shoreline because seaweeds are confined by their light requirements essentially to the littoral or shallow sublittoral zones. It is by no means certain that such sediments will have retained much of their original organic matter produced by decaying vegetation, *pace* the Termiers, since only slight changes of environment could result in strong wave or current action and strongly oxidizing conditions in such a régime as this.

The complication of evolutionary size changes. Increase or decrease in size during the course of evolution is familiar in fossil vertebrates and is no less true for many invertebrate (Newell 1949). That this may have operated even intraspecifically is suggested by detailed work on the Blue Lias in southern Britain (Hallam 1960). As much as a fourfold regional increase in size up the succession (which is probably valid for much of Europe as well) was discernible in a number of molluscan species. This was not evidently related to sedimentary facies and environmental control over such a large area could reasonably be discounted. When, as in this case, appreciable changes take place

TABLE 1

Environment	*Associated Faunal Characteristics*	*Sediment Type*	*Remarks*
Low salinity	Numerical abundance coupled with restriction in variety. Stenohaline forms (corals, brachiopods except *Lingula*, cephalopods, echinoderms, bryozoa, &c.) rare or absent.	Deltaic associations indicative of fluvial influx into sea or lagoon; beds of coal or lignite as indicators of humidity. Distinctive geochemical characteristics, e.g. high boron content of illite.	An important factor, which may produce strong size gradients within a small area or in a thin succession of strata. Comparatively well documented.
High salinity	As above.	Associated evaporitic and dolomitic carbonate deposits as indicators that evaporation exceeded precipitation.	Not well documented at present but probably important locally.
Oxygen deficiency	Restricted in variety. Relatively high percentage of nektonic and planktonic forms, with burrowers (endobionts) rare or absent. Surface-living benthos thin-shelled, with little indication of much physical disturbance after death. Well-preserved vertebrates.	Characteristically fine-grained (shales or limestones) with abundance of bituminous matter and/or pyrite. Fine sedimentary lamination, with organic layers, common.	Probably one of the most important factors in the past, when restricted sedimentary basins were common. A large literature.
High turbidity	Relative abundance of forms adapted to a soft bottom, e.g. burrowing lamellibranchs. Relative rarity of forms requiring clear water, e.g. colonial corals, brachiopods, or a hard substratum, e.g. most gastropods. Disturbance after death relatively slight.	Beds finer grained, more argillaceous or thicker than associated beds with larger fossils of same species. Allowance should be made for differential compaction in assessing differences of thickness.	May be very important, especially for comparatively slight differences in size, but is not well documented and is greatly in need of further intensive study. Stunting is probably confined to suspension feeders.
Strong water agitation	Fossils will tend to have robust skeletons and certain groups such as corals and sponges will have special growth forms. Physical adaptation may be extreme, as in patelliform gastropods. High incidence of fragmentation.	Biohermal, skeletal, oolitic, and detrital limestones characteristic, perhaps with associated sandy and conglomeratic beds.	In this environment, demanding extreme adaptation, only a small proportion of fauna may exhibit stunting. Problem of size selection of juveniles is here especially acute.
High population density	Masses of shells crowded together may on rare occasions be preserved as original life assemblages, e.g. barnacles on large shells or stones.	No particular correlation, but beds in which shell density is high because of low sedimentary rate should be firmly excluded from consideration.	Will normally be difficult or impossible to detect because of disturbance of fossils after death.
Temperature variations	Stunted fossils in presumed higher latitudes should be associated with fauna of restricted diversity but containing stenohaline forms, if their optimum environment is in warmer water, but other species may have had their optimum in cooler water.	No particular correlation, except a very general one based on sediment associations as palaeoclimatic indicators, e.g. limestones signifying warm seas, glacial deposits signifying cold conditions.	May be important for individual species but a general rule is not discernible. Size gradients in a restricted area likely to be small.
Deficient food supply	Fossils will probably be sparse in numbers as well as small in size.	No particular correlation, but more likely in fine-grained sediments signifying weak currents, and deep-water sediments. Sediments rich in organic matter should be excluded from consideration, stunting here being indicative of a reduced capacity to feed.	Although this involves the primary factor, it will in most cases be impossible to detect.

within the confines of a single formation there is a serious danger of misinterpretation unless the factor of evolution is taken into account.

It is quite conceivable that many of the small Triassic fossils discussed by Boni (1942) are of the normal size for the stage of evolution to which they belong (cf. Kummel 1948).

CONCLUDING REMARKS

If the interpretations in this review are hedged with qualifications it is not merely because the many variables are sometimes difficult to disentangle and the data often inadequate. It is also the result of the diversity of organic adaptation. If there is any really general rule in this respect, it is that if an environment exists that is tolerable to life, even though generally regarded as unfavourable, there will be some organisms that flourish in that environment. Thus although most marine invertebrates react adversely to brackish water there will always have been some that have achieved a good adaptation and hence will not exhibit a stunting of growth, just as others can live apparently little-affected under conditions of low oxygen tension. Therefore in this field one cannot be hopeful that further research will always produce high correlations or clear-cut results; it is more likely that the exercise of judgement and discretion will continue to play a major role in interpretation. In particular, knowledge of variation of the primary factor in stunting, food supply, is likely to remain elusive to palaeoecologists.

Nevertheless, it is clear that a considerable research field exists that has hitherto been scarcely touched upon. More critical work is required on both recent and fossil faunas. There is a strong need for further experiments on living species and quantitative data on both the size of organisms and their environment. In the case of fossils criteria of maturity should be sought where possible and the rock from which they were collected fully described. The author's interpretation of the principal environmental causes of stunting, and the main criteria by which they may be distinguished, is summarized in Table 1.

The study of suspected stunting in fossils can hardly fail to be rewarding, since even a rejection of stunting in favour of immaturity, if based on sound evidence, will provoke fresh problems, the solution of which may prove equally illuminating.

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